

A DEMOGRAPHIC AND LANDSCAPE ANALYSIS FOR
COMMON LOONS IN NORTHWEST MONTANA

By

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ABSTRACT

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A Demographic and Landscape Analysis for Common Loons in Northwest Montana

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Understanding the relationship between a species' important vital rates and how they respond to environmental factors is essential for developing appropriate conservation strategies. Historically, breeding populations of common loons existed across much of the northwestern United States, but that area of distribution within the lower 48 states has been significantly reduced. Montana still has the largest breeding population of common loons in the western continental United States, averaging 40-70 territorial pairs annually. Most research to date on loon population dynamics, habitat use, and response to disturbance was conducted in much larger populations of the Midwest and Northeast United States and did not account for individual vital rate importance. Recent sensitivity analysis showed that fecundity was the vital rate had the most influence on the population growth rate in common loons. Therefore, I designed my research to evaluate the relationships between disturbance (as measured by the number of houses, resorts, and campgrounds in relation to lake size), habitat, intraspecific interactions and territory occupancy and reproduction. I used occupancy models to explore the dynamics underlying occupancy of potential lakes. I observed that landscape scale effects were important to occupancy of loon territories. The abundance of feeding lakes and the number of territorial pairs within 10 km were equally important for explaining probabilities of occupancy. I suggest managers protect both occupied, as well as, unoccupied lakes, especially when in close proximity to clusters of territorial pairs and feeding lakes. I observed that lake scale effects were more important to reproductive potential than landscape scale effects. I found a significant negative relationship with islands and a significant positive relationship with shoreline complexity on reproduction. Shoreline disturbance did not appear important when compared to other factors, but there are factors associated with Montana's outreach and education program that probably affected this result. For increasing reproduction I suggest managers continue current management activities, but include a greater focus on protecting nesting habitat on lakes without islands. I also suggest managers continue to mitigate for disturbance while exploring other ways to evaluate the effects of disturbance on occupancy and reproduction.

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Christopher Allan Moanikeala Hammond
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INTRODUCTION

The global population of common loons (*Gavia immer*) is considered “secure” (IUCN G5 Ranking); however, many local populations are small, isolated, and vulnerable to extinction primarily due to habitat loss and human encroachment into key habitats (Kelly 1992, Evers 2004). Loons are considered imperiled (MT ranking S2) by the Montana Natural Heritage Program and are listed as a “sensitive species” by the U.S. Forest Service in Region 1. In the lower 48, Minnesota has the largest population of common loons with 10,355-12,897 followed by Maine, Wisconsin, Michigan and New York with approximately 4,100, 3,131, 1,937 and 1,036 respectively (Evers 2004). In the western continental US, Montana has the largest population of common loons, averaging 180-200 birds annually (Bissell 2005). Wyoming has about 54 loons and Idaho and Washington (the common loon is a State Candidate Species in WA) each have only about 12 adults (Evers 2004).

Understanding the relationship between important vital rates and how they respond to environmental factors is essential for developing appropriate conservation strategies. Most research to date on loon population dynamics, habitat use, and response to environmental factors was conducted in much larger populations of the Midwest and northeast United States, did not account for individual vital rate importance, and thus may not be applicable to Montana. Recent sensitivity analysis for the Montana population showed that fecundity was the vital rate had the most influence on the population growth in common loons. Current management strategies in Montana focus on maximizing chick production by mitigating for human disturbances, which are generally quantified as ratios of shoreline development (private and public) to surface area or perimeter (Vermeer 1973).

Loons are becoming increasingly affected by human disturbance inducing a decline in breeding populations in several areas (Caron and Robinson 1994, Clay and Clay 1997, Piper et al. 2002, Titus and VanDruff 1981, Vermeer 1973). Common loons tend to nest on fishing lakes throughout their breeding grounds, which also tend to have the highest recreational use (Titus and VanDruff 1981, Vermeer 1973). The loon's response to human recreational disturbance includes vocalizations, physical displays, and most detrimental, nest flushing (Titus and VanDruff 1981, Vermeer 1973). When adults are flushed from the nest, eggs become vulnerable to predation by bald eagles (*Haliaeetus leucocephalus*), common ravens (*Corvus corax*), and American crows (*Corvus brachyrhynchos*) (Alvo 1981, Alvo and Blancher 2001, Croskery 1991, Titus and VanDruff 1981). In addition, eggs may be knocked off the nest or cool down if the adult is off the nest too long (Croskery 1991). Human encroachment on nesting habitat and disturbance continue to jeopardize common loon populations (Christenson 1981, Heimberger et al. 1983, Kelly 1992, Sutcliffe 1980). To date, most research on common loons in the U. S. has been limited to the Midwest and the Northeast (Evers 2004). Of the recent habitat research, none has linked their results to landscapes for use as a conservation planning tool (Newbrey 2002, Paugh 2006).

Since we were interested in protecting resources that contribute to the longevity of common loons, it was logical to address long-term management needs by investigating both demographic and landscape relationships responsible for current population levels and distribution. Our research was designed to 1) address how population dynamics (i.e. fecundity, occupancy, and stability) were linked to territory distribution and abundance, 2) address how population dynamics were related to habitat, disturbance, and intraspecific competition, 3)

address how population dynamics were related to lake and landscape scales effects, and 4) estimate occupancy, colonization, and abandonment rates of lakes.

In this chapter, we provide background and justification for our research. In the second chapter we use a patch occupancy approach to investigate the territory occupancy dynamics of over 200 lakes in northwest Montana. We estimate the probability of occupancy for individual territories throughout the entire known breeding range of common loons in the state. We examine rates of colonization and abandonment across the landscape and how all rates are related to lake scale and landscape scale effects, as well as, habitat, disturbance, and intraspecific competition. In the third chapter, we evaluate a candidate set of a priori modes to identify factors influencing fecundity on individual territories. We also explore the importance of lake scale and landscape scale effects. Last, in the appendix we provide an estimate of survival for breeding adults from the marked population in northwest Montana.

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RH: Common Loon Territories• Hammond et al.

TERRITORY OCCUPANCY BY COMMON LOONS IN RESPONSE TO DISTURBANCE, HABITAT, AND INTRASPECIFIC RELATIONSHIPS

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ABSTRACT We created and tested occupancy models that evaluated the hypothesized effects of disturbance, habitat, and intraspecific relationships on territory occupancy by common loons (*Gavia immer*) in Montana. We visited potential lakes multiple times and classified them as occupied or unoccupied. Model averaged results indicated that the abundance of feeding lakes within 10 km and the number of territorial pairs were both equally important for explaining probabilities of occupancy. We had substantial support that the population was in a state of equilibrium. We suggest that best management strategy for stable populations is long term monitoring and protection of territorial lakes and feeding lakes as these two factors have the most influence on the probability of occupancy of surrounding lakes. The levels of disturbance (as measured by the number of houses, resorts, and campgrounds in relation to lake size) we

observed did not appear important compared to other factors; however, we contribute this result to mitigation efforts such as placing buoys around nest sites and public outreach put in place over 15 years. We recommend managers continue to mitigate for disturbance while exploring other options for evaluating disturbance effects on occupancy.

KEY WORDS common loon, colonization, extinction, *Gavia immer*, habitat, management, Montana, occupancy, territory.

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Historically, breeding populations of common loons existed across much of the northwestern United States (Evers 2004). Montana has the largest breeding population of common loons in the western continental United States, averaging 40-70 territorial pairs annually (G. N. Bissell, Montana Department of Fish, Wildlife, and Parks, unpublished report). Wyoming averages about 19-25 territorial pairs annually while Washington has < 5 (Evers 2004). Taylor (J. Taylor, Idaho Department of Fish and Game, unpublished report) documented successful breeding on two lakes in northern Idaho. Breeding populations in Oregon and California were extirpated during the mid-1900s (Evers 2004). Many local breeding populations are small, isolated, and vulnerable to extinction primarily due to decreasing numbers of territories caused by habitat loss and human encroachment into key habitats (Kelly 1992, Evers 2004).

Since the mid 1980s, volunteers and biologists have collected territory and reproductive data for lakes in northwest Montana in an attempt to understand breeding habitat selection and how it is linked to quantity and distribution of potential habitat. In 1990, the Montana Common Loon Management Plan was completed which estimated approximately 57 current and 128 potential territories (Skaar 1990). The creation of the Montana Common Loon Working Group in 1999 increased and focused monitoring efforts to collect annual data on numbers of breeding

pairs and reproduction. Additionally, the working group created an internship program to mitigate disturbance during the nesting season to promote nest survival, chick survival, fledging success, and territory occupancy. Over 200 lakes are surveyed twice annually; once in the spring (usually prior to nest hatch in mid-May) and once in the summer (usually post hatch in mid-July; G. N. Bissell, Montana Department of Fish, Wildlife, and Parks, unpublished report). The data collected between 1999-2006 indicate the number of occupied territories consistently averaged between 40-60 (G. N. Bissell, Montana Department of Fish, Wildlife, and Parks, unpublished report) with no obvious expansion, suggesting that Montana's population may be in an equilibrium state (i.e. realized maximum occupancy potential, or carrying capacity). If the population is in an equilibrium state then under current conditions we would expect that the population is responding to the configuration of territories and not the quantity of territories, and thus we would not observe territory expansion.

Numerous factors can drive territory occupancy by common loons and relate primarily to nest success and chick survival (Olson and Marshall 1952, Vermeer 1973, Sutcliffe 1980, Titus and VanDruff 1981, Kelly 1992, Evers 2004, Paugh 2006). Large lakes may offer loons more suitable and protected locations for nest sites and nurseries (McIntyre 1983, McIntyre and Barr 1997, Evers 2001), as well as reduce a loon's exposure to disturbance, and provide critical littoral areas for foraging (Skaar 1990, Evers 2004). The same holds true for lakes with complex shorelines and bays (Newbrey 2002). For nesting habitat, loons tend to select islands for nest locations over shoreline nests (Olson and Marshall 1952, Vermeer 1973, Sutcliffe 1980, Titus and VanDruff 1981, Kelly 1992) where they generally have higher nest success (Titus and VanDruff 1981). Nest success may decrease when loons are exposed to disturbance (Vermeer 1973, Kelly 1992). Loons can adapt to disturbance (Titus and VanDruff 1981); however, they

spend more time off the nest leaving eggs vulnerable to predators (Christenson 1981). In addition, recruitment may decline as fewer loons are likely to return to breed in areas with excessive disturbance (Vermeer 1973).

Few studies have investigated territory selection in common loons, (Strong 1985, Newbrey 2002) and no research has been conducted to assess the influence of both local and landscape-scale factors on territory occupancy, colonization, and extinction (hereafter referred to as abandonment). Since loons are visual predators, the clarity of a lake (Barr 1986) may play an important role in territory selection. Territory selection may also be influenced by the abundance of feeding lakes and the number of territorial pairs within 10km (Paugh 2006) and distance to the nearest territorial pair as loons must actively defend territories throughout the breeding season and areas with higher densities of loons may experience reduced productivity (Evers 2004). With recent advances in modeling techniques researchers can now incorporate characteristics like these into models and explore the potential patterns and dynamics underlying the occupancy of patches and territories (MacKenzie et al. 2006).

Rates of occupancy, colonization, and abandonment provide valuable information about factors influencing population distribution and over all population status. In this paper we investigated the influence of habitat, disturbance, and intraspecific competition on rates of occupancy, colonization, and abandonment. We created and tested a priori biologically relevant models and compared individual factors to their hypothesized effects (Table 1). In addition, we compared lake scale and landscape scale effects on occupancy rates.

STUDY AREA

Our study area covered approximately 63,500 km² in northwestern Montana (Figure 1). Lake sizes ranged from 0.05 km² to 27.29 km² and were surrounded by many different landowners

including the United State Forest Service (USFS), Montana Department of Natural Resources and Conservation, MFWP, Plum Creek Timber Company, Glacier National Park, Blackfeet Indian Reservation, and many individual private landowners. Typical types of human disturbance included shoreline development, fishing, canoes, kayaks, jet skis, other forms of high speed water recreation. Land use practices varied by landowner and included agricultural uses, timber harvest, allotment grazing, recreation, and development. Vegetation ranged from mixed conifer forests in the mid to high elevations to cottonwood and willow stands along riparian corridors. Elevations ranged from 670 m to 1676 m.

METHODS

Covariate Data Collection

We created a Geographic Information System (GIS) and used size, elevation (Skaar 1990), location (Skaar 1990, Kelly 1992, Paugh 2006), and water fluctuation (e.g. reservoirs or sloughs) as criteria to identify potential lakes for sampling. We removed lakes below 5 ha (0.4 ha below the known lower limit for nesting lakes in Montana; Skaar 1990, Kelly 1992) and all lakes above 1524 m (Skaar 1990). All nesting occurred in seven counties in the northwestern portion of the state. Rather than use geopolitical boundaries (i.e., county lines) as the location criteria, we used ecological unit subsections in which loons nested (Nesser et al. 1997). We systematically removed lakes and sloughs connected to regulated rivers because of unnatural water level fluctuation which prevents natural nesting. We visited each potential lake and collected data for covariates to assess factors affecting occupancy, extinction, and colonization (Table 1). To calculate disturbance ratios we assigned 10 points to each government campgrounds or private resorts, 5 points to each public accesses not maintained, and 1 point for each house bordering a

lake and then divided the total disturbance points by the lake surface area and lake perimeter Vermeer (1973).

Lake Surveys

Since loons tend to remain at or near carrying capacity (Evers 2004), exhibit high territory fidelity with obvious territorial calls and displays (Evers 2001), and were monitored over the last 20 years in Montana, we assumed if a pair was present on a lake we would observe the pair or find its nest. They are an aggressive species with obvious territorial calls and displays, so that the presence of pair on a lake makes it likely to observe the pair or find its nest. Common loons are an aggressive, territorial species with obvious territorial calls and displays; therefore, we assumed if a pair was present on a lake we would observe the pair or find its nest. Each field season we began searching for occupied lakes during the first week of May beginning with lakes historically occupied by loons followed by the additional potential lakes. We surveyed lakes with 20X-60X spotting scopes. Large lakes with complex shorelines were surveyed by boat or kayak. Lakes were generally visited at least twice each season with some exceptions.

Data Analysis

Modeling occupancy, colonization, and abandonment.— We assigned variables into one of three model categories: disturbance, habitat, and intraspecific interaction (Table 1). We also categorized variables as either lake or landscape scale (Paugh 2006). We used Pearson correlation coefficients to measure the relationships between all possible combinations of variables. For variables where $r \geq 0.6$, we chose to included only the variable that had the most biological meaning base on previous common loon habitat studies. We estimated occupancy and detection probabilities using a model-based approach described by MacKenzie et al. (2006). This approach allowed for simultaneous parameter estimation that allowed easy comparison of

competing hypotheses using model selection. We removed 64 lakes from the analysis because they were visited only in 2007 and in some instances only once (MacKenzie and Bailey 2004). Common loons are a territorial species with high site fidelity (Evers 2004, MFWP unpublished data); therefore, we used models that assume that the probability that a territory is occupied in a season depends on its occupancy status the previous season (MacKenzie et al. 2006). We calculated naïve occupancy, which assumes a detection probability equal to 1 and estimated true occupancy by incorporating the estimated detection probability. We defined individual territory occupancy as the probability that a random territory was occupied by at least one territorial pair, while colonization was defined as the probability that an unoccupied territory became occupied the following year, and extinction was defined as the probability that an occupied territory became unoccupied the following year, hereafter referred to as abandonment. We estimated territory occupancy, colonization, and abandonment with unconditional explicit dynamic models in Program PRESENCE 2.0 (Hines and MacKenzie 2004) that allowed us to incorporate covariates and data with missing observations leading to more biologically plausible models (MacKenzie et al. 2006). We used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank all models within individual categories and over all categories (Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2$ have substantial support while model with $4 \leq \Delta AIC_c \leq 7$ receive considerably less (Burnham and Anderson 2002). We used model weights to evaluate relative support among models, and model-averaged coefficients to reduce variability of predicted values and increase model-based inference for prediction (Burnham and Anderson 2002). We calculated variable importance to assess the relative contribution of the covariates to the model.

Model testing.—We used averaged coefficients of models with $\Delta AIC < 4$ to estimate the probability of occupancy on an independent data set of 36 lakes and compared the estimated probabilities to actual occupancy data. We used the Receiver Operating Characteristic (ROC) statistic to assess the fit of the model to the data (Hosmer and Lemeshow 2000). The ROC represents a measure of discrimination where $ROC = 0.5$ is equivalent to flipping a coin whereas $0.7 \leq ROC \leq 0.8$ is considered acceptable discrimination, $0.8 \leq ROC \leq 0.9$ is considered excellent discrimination, and $ROC \geq 0.9$ is considered outstanding discrimination (Hosmer and Lemeshow 2000).

RESULTS

We observed territorial pairs on 47 lakes in 2006 and 57 lakes in 2007, resulting in naïve occupancy estimates of 22.8% and 27.7% of available territories and estimated true occupancy was 26.2% and 32.0%, respectively. Colonization was constant in 4 out of 5 of the top models. It was associated with disturbance and shoreline complexity in the remaining model.

Abandonment was constant in 2 out of 5 models. It was associated with only intraspecific covariates in the remaining 3 models (Table 2). Intraspecific models ranked highest among categories. Disturbance categories were second with the highest ranking disturbance model ranked 10th overall ($\Delta AIC_c = 6.76$). Habitat categories were last with the highest ranked habitat model 17th overall ($\Delta AIC_c = 9.21$). In addition, models with lake scale covariates received little support while models with landscape scale covariates received considerable support.

Model selection identified 5 competing models ($\Delta AIC_c < 4$) which included only intraspecific covariates and accounted for 79.1% of model weight. Model averaged estimates revealed a significant positive effect of number of territorial pairs within 10 km and significant negative effect of the abundance of feeding lakes within 10 km (Table 3). The number of

territorial pairs and feeding lakes within 10 km were equally important in explaining occupancy (variable importance = 0.79); however, territorial pairs within 10 km had a positive effect whereas feeding lakes within 10 km had a negative effect. The distance to the nearest territorial pair was considerably less important (variable importance = 0.20) and negatively associated with occupancy. An ROC analysis on our test subset yield an ROC = 0.68.

DISCUSSION

From 1987 to 2005 the number of annually occupied territories in Montana was 40-60 with no obvious trend. We were interested in investigating whether the population was growing, declining, or stable and what factors might be influencing the quantity and distribution of territories on the landscape. Models indicated that the occupancy of common loon territories in Montana was stable. Our top 5 models explained most of the variation in the data suggesting we captured most of the influential factors that explain why potential habitat remains unoccupied. Four of our top 5 occupancy models were essentially variations of only 2 models where the only difference was that the abandonment parameter was constant. Adding additional parameters for abandonment did not improve the fit over the constant model providing additional support for models where colonization and abandonment were constant and suggesting that the population was in a state of equilibrium. Our number of naïve estimate of occupied territories (57 in 2007) was consistent with previous common loon territory estimates for Montana (57 in 1989) (Skaar 1990). However, after accounting for probability of detection, our estimated true occupancy was 66 territories, suggesting that even though the species is easily detected we are not observing the all territorial pairs in Montana.

The number territorial pairs within 10 km and abundance of feeding lakes within 10 km were equally important in explaining occupancy in common loon territories suggesting that the

system is potentially responding to a more complex intraspecific interaction. The distance to the nearest territorial pair was considerably less important and its effect was ambiguous as the confidence interval for coefficient estimates overlapped 0. Previous research suggested loons were poor dispersers with high territory fidelity (Evers 2001) that may explain why our hypothesized positive association with the number of territorial pairs was supported by the data. Poor dispersal and territory fidelity may also explain why our hypothesized positive effect of feeding lakes on occupancy was contradicted by the data and suggested a negative relationship. Single loons tend to congregate on feeding lakes making them difficult to defend as territories. In addition, loons may use feeding lakes while trying to takeover established territories rather than establishing new territories thus reducing the probability of occupancy.

We expected disturbance to rank high for its influence on occupancy rates, but disturbance models received very little support. We hypothesize that disturbance models ranked low because of current mitigation. Kelly (1992) reported an increase in productivity on several lakes in northwest Montana after implementing information and education programs and deploying floating signs around nests. We believe it is possible that the continuation of these efforts have been successful in mitigating the potential negative effects of disturbance on reproductive potential. We feel other measures of human disturbance, such as user hours might yield different results. Paugh (2006) showed a negative relationship between mean angler trips and chick survival. However, the extent of our study area and number of study lakes prevented us from collecting this type of user related data.

Our results support that the influence of the spatial arrangement of territories on selection behavior in common loons has more influence on occupancy dynamics than the abundance of available territories. Of the 206 lakes surveyed more than 72% were unoccupied. This was

similar to observations of Skaar (1990) who surveyed 185 lakes of which 69% were unoccupied. Loons are poor dispersers and may be choosing new territories based on proximity to occupied territories which may explain why probabilities of occupancy are high in nearby potential territories. We acknowledge that because of the limited duration of our study that adequate time may not have been available to observe expansion into potential habitat. However, the lack of change in number of occupied territories over 20 years supports our findings that spatial arrangement of occupied territories is driven by intraspecific interactions that are likely influencing the equilibrium in the occupancy of territories in Montana.

We collected our data in a system where loons generally occupied and defended a single lake and we had very few lakes containing multiple pairs. For this reason we suggest our models may not be appropriate for predicting occupancy in systems where numerous lakes have multiple pairs, especially if the number per lake exceeds 4 pairs.

MANAGEMENT IMPLICATIONS

Our results suggest that the factors that most influence occupancy of territories by common loons are the number of territorial pairs and abundance of feeding lakes within 10 km. We suggest that managers prioritize conservation efforts by targeting lakes that have high numbers of territorial pairs and low numbers of feeding lakes in the surrounding landscape. We hypothesize that the result of little support for disturbance is related to the mitigation practiced over the last several years and suggest that the Montana Common Loon Working Group, through interns with multiple partners, continue to provide public education regarding loon nesting ecology on lakes with breeding loons, place floating signs to implement voluntary nest site closures, give campfire presentations, and collect vital information on lake use.

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TABLES AND FIGURES

Table 1. Definitions of disturbance, habitat, and intraspecific variables that we evaluated and their hypothesized effects on occupancy, colonization, and abandonment for territories of common loons in northwest Montana, USA, 2006-2007.

Table 2. Summary of model selection results ($\Delta AIC < 4$) for territory occupancy by common loons on lakes in northwest Montana, USA, 2006-2007. Occupancy is represented by Ψ , colonization is represented by γ , and extinction is represented by ϵ . The number of territorial pairs within 10 km is TP10, the number of feeding lakes within 10 km is FL10, the distance to the nearest territorial pair is DTTP, and disturbance is VDRPER.

Table 3. Coefficient estimates (SE) from the model averaged model (Akaike wt = 0.791) describing territory occupancy for common loons, northwest Montana, USA, 2006-2007.

Fig. 1. Common loon research area, Montana, USA, 2006-2007.

Table 1.

Model Category	Variable Scale	Definition	Hypothesized Effect		
			Ψ	γ	ε
Disturbance	Lake	Disturbance ratio of human development and recreation use on lake in relation to surface area ^a	$\beta < 0$	$\beta > 0$	$\beta > 0$
Habitat	Lake	Disturbance ratio of human development and recreation use on lake in relation to perimeter	$\beta < 0$	$\beta > 0$	$\beta > 0$
	Lake	Shoreline complexity	$\beta > 0$	$\beta > 0$	$\beta > 0$
	Lake	Presence of islands	$\beta > 0$	$\beta > 0$	$\beta > 0$
	Lake	Water clarity measure by Secchi Disk	$\beta > 0$	$\beta > 0$	$\beta > 0$
	Lake	Lake surface area	$\beta > 0$	$\beta > 0$	$\beta > 0$
	Lake	Lake perimeter ^b	$\beta > 0$	$\beta > 0$	$\beta > 0$
Intraspecific	Landscape	Number of territorial pairs within 10 km	$\beta > 0$	$\beta > 0$	$\beta > 0$
	Landscape	Number of feeding lakes within 10 km	$\beta > 0$	$\beta > 0$	$\beta > 0$
	Landscape	Distance to the nearest territorial pair	$\beta > 0$	$\beta > 0$	$\beta > 0$

^a We excluded surface area disturbance ratio from the analysis because of its correlation with the perimeter disturbance ratio ($r = 0.65$).

^b We excluded lake perimeter from the analysis because of its correlation with lake surface ($r = 0.94$) and shoreline complexity ($r = 0.65$).

Table 2.

Model	K	AIC _c	Within category Δ AIC _c	Within category w	All categories Δ AIC _c	All categories w
Intraspecific						
$\Psi(\text{TP10+FL10})\gamma(.)\varepsilon(\text{TP10+DTTP})p(.)$	6	616.13	0	0.4054	0	0.3851
$\Psi(\text{TP10+FL10})\gamma(.)\varepsilon(.)p(.)$	5	617.71	1.58	0.1841	1.58	0.1748
$\Psi(\text{TP10+FL10+DTTP})\gamma(.)\varepsilon(\text{TP10+DTTP})p(.)$	7	618.34	2.21	0.1341	2.21	0.1274
$\Psi(\text{TP10+FL10})\gamma(\text{VDRPER+SDI})\varepsilon(\text{TP10+DTTP})p(.)$	7	619.91	3.78	0.0612	3.78	0.0581
$\Psi(\text{TP10+FL10+DTTP})\gamma(.)\varepsilon(.)p(.)$	6	619.94	3.81	0.0604	3.81	0.0573
Disturbance						
$\Psi(\text{VDRPER})\gamma(.)\varepsilon(\text{TP10+DTTP})p(.)$	5	622.89	0	0.4479	6.76	0.0131
$\Psi(\text{VDRPER})\gamma(.)\varepsilon(.)p(.)$	4	625.75	2.87	0.1069	9.63	0.0031
$\Psi(\text{VDRPER})\gamma(\text{VDRPER+SDI})\varepsilon(\text{TP10+DTTP})p(.)$	6	626.49	3.58	0.0748	10.34	0.0022
$\Psi(\text{SDI})\gamma(.)\varepsilon(\text{TP10+DTTP})p(.)$	5	627.12	4.23	0.054	10.99	0.0016
$\Psi(\text{VDRPER})\gamma(\text{VDRPER+SDI})\varepsilon(.)p(.)$	5	627.48	4.59	0.0451	11.35	0.0013
Habitat						
$\Psi(\text{LNSA+ISL})\gamma(.)\varepsilon(\text{TP10+DTTP})p(.)$	6	625.34	0	0.1567	9.21	0.0039
$\Psi(\text{LNSA})\gamma(.)\varepsilon(\text{TP10+DTTP})p(.)$	5	625.99	0.65	0.1132	9.86	0.0028
$\Psi(\text{CLR})\gamma(.)\varepsilon(\text{TP10+DTTP})p(.)$	5	626.19	0.85	0.1025	10.06	0.0025
$\Psi(\text{ISL})\gamma(.)\varepsilon(\text{TP10+DTTP})p(.)$	5	627.33	1.99	0.0579	11.2	0.0014
$\Psi(\text{SDI+ISL})\gamma(.)\varepsilon(\text{TP10+DTTP})p(.)$	6	627.46	2.12	0.0543	11.33	0.0013

Table 3.

Covariate	Estimate	SE	Upper 95% CI	Lower 95% CI
TP10 ^a	0.260	0.097	0.411	0.033
FL10 ^b	-0.163	0.051	-0.063	-0.263
DTTP ^c	-0.001	0.004	0.008	-0.010

^a TP10 = number of territorial pairs within 10 km.

^b FL10 = number of feeding lakes within 10 km.

^c DTTP = distance to the nearest territorial pair.

Figure 1.



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RH: Common Loon Reproduction Potential • Hammond et al.

REPRODUCTIVE POTENTIAL OF COMMON LOONS IN NORTHWEST MONTANA

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ABSTRACT We created models that evaluated the effects of disturbance, habitat, and intraspecific relationships on reproduction by common loons (*Gavia immer*) in Montana. We visited territorial lakes multiple times and recorded fledgling production. Based on statewide fecundity estimates, Montana's loon population is increasing slightly ($\lambda = 1.02$). Model averaged results indicated that the presence/absence of islands was most important for explaining reproductive potential while shoreline complexity was also important, but to a lesser extent. Lakes without islands fledged more young than lakes with islands. We recommend that managers conserve shoreline habitat especially on lakes without islands and that have convoluted shorelines. The effect of disturbance on reproduction was ambiguous. We suggest that disturbance mitigation efforts enacted

over 15 years ago continue to show benefits today and therefore, suggest that managers continue mitigation.

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KEY WORDS Common Loon, disturbance, fecundity, *Gavia immer*, habitat, management, Montana, reproduction.

Historically, breeding populations of common loons existed across much of the northwestern United States (Evers 2004). Montana has the largest breeding population of common loons in the western continental United States, averaging 40-70 territorial pairs annually (G. N. Bissell, Montana Department of Fish, Wildlife, and Parks, unpublished report). Wyoming averages about 19-25 territorial pairs annually while Washington has < 5 (Evers 2004). Taylor (J. Taylor, Idaho Department of Fish and Game, unpublished report) documented successful breeding on two lakes in northern Idaho. Breeding populations in Oregon and California were extirpated during the mid-1900s (Evers 2004). Many local breeding populations are small, isolated, and vulnerable to extinction primarily due to decreasing numbers of territories in response to disturbance (Kelly 1992, Evers 2004), generally quantified as ratios of water recreation and shoreline development to surface area or perimeter (Vermeer 1973).

Since the mid 1980s, volunteers and biologists have collected territory and reproductive data for lakes in northwest Montana to understand reproductive potential and how it is linked to disturbance and the quantity and distribution of potential habitat. In 1990, the Montana Common Loon Management Plan was completed which estimated approximately 57 current and 128 potential territories (Skaar 1990). The creation of the Montana Common Loon Working Group in 1999 increased and focused monitoring efforts to collect annual data on numbers of breeding

pairs and reproduction. Over 200 lakes are surveyed twice annually; once in the spring (usually prior to nest hatch in mid-May) and once in the summer (usually post hatch in mid-July; G. N. Bissell, Montana Department of Fish, Wildlife, and Parks, unpublished report). The data collected during 1999-2006 indicates the number of chicks fledged consistently ranged between 35-55 (G. N. Bissell, Montana Department of Fish, Wildlife, and Parks, unpublished report).

Many studies have documented habitat, disturbance, and intraspecific characteristics of nesting lakes in relation to nest success and chick survival (Olson and Marshall 1952, Vermeer 1973, Sutcliffe 1980, Titus and VanDruff 1981, Kelly 1992, Evers 2004, Paugh 2006). Large lakes may offer loons more suitable and protected locations for nest sites and nurseries (McIntyre 1983, McIntyre and Barr 1997, Evers 2001), as well as reduce a loon's exposure to disturbance, and provide critical littoral areas for foraging (Skaar 1990, Evers 2004). The same holds true for lakes with complex shorelines and bays (Newbrey 2002). For nesting habitat, loons tend to select islands for nest locations over shoreline nests (Olson and Marshall 1952, Vermeer 1973, Sutcliffe 1980, Titus and VanDruff 1981, Kelly 1992) because islands generally have higher nest success (Titus and VanDruff 1981). Paugh (2006) observed higher nest success on artificial platforms than on natural islands or shoreline nests. Nest success may decrease when loons are exposed to disturbance (Vermeer 1973, Kelly 1992). Loons can tolerate disturbance (Titus and VanDruff 1981); however, they spend more time off the nest leaving eggs vulnerable to predators (Christenson 1981). In addition, recruitment may decline as fewer loons are likely to return to breed in areas with excessive human disturbance (Vermeer 1973). Since loons are visual predators, the clarity of a lake (Barr 1986) may play an important role in territory selection. Nest survival and chick survival may also be influenced landscape scale effects like the abundance of feeding lakes and the number of territorial pairs within 10km (Paugh 2006) and

distance to the nearest territorial pair as loons must actively defend territories throughout the breeding season and areas with higher densities of loons may experience reduced productivity (Evers 2004).

Understanding the relationship between important vital rates and how they respond to environmental factors is essential for developing appropriate conservation strategies. We used life-stage simulation analysis (Wisdom and Mills 1997, Mills 2007) to estimate that the vital rate with the most influence on population growth in common loons in Montana was fecundity (# female chicks/territorial pair) (Hammond unpublished data). Likewise, Evers (2004) illustrated with his population model that common loon populations need to have a reproductive potential of at least 0.24 female chicks fledged/territorial pair to remain stable (i.e., population growth rate, $\lambda=1$). Fecundity values from across the United States and Canada ranged from 0.14 to 0.48 (Evers 2004).

We quantified territory specific reproductive potential as the number of female fledglings produced each year for each territory (hereafter referred to as reproduction). Reproduction is a valuable measure to assess population status and when examined at the territory level can provide valuable insight into management recommendations. To adequately investigate potential reproduction, we developed a priori hypotheses based on the response of fecundity to three categories of variables: disturbance, intraspecific competition, and habitat (Table 1). Thus we designed our research to answer the following questions: 1) what was influencing reproductive potential, 2) did unoccupied territories have lower reproductive potential than occupied territories, 3) did the spatial arrangement of occupied territories influence the reproductive potential of territories, and 4) was Montana's population increasing, decreasing, or stable?

STUDY AREA

Our study area covered approximately 63,500 km² in northwestern Montana (Figure 1). Lake sizes ranged from 0.05 km² to 27.29 km² and were surrounded by many different landowners including the United State Forest Service (USFS), Montana Department of Natural Resources and Conservation, MFWP, Plum Creek Timber Company, Glacier National Park, Blackfeet Indian Reservation, and many individual private landowners. Typical types of human disturbance included shoreline development, fishing, canoes, kayaks, jet skis, other forms of high speed water recreation. Land use practices varied by landowner and included agricultural uses, timber harvest, allotment grazing, recreation, and development. Vegetation ranged from mixed conifer forests in the mid to high elevations to cottonwood and willow stands along riparian corridors. Elevations ranged from 670 m to 1676 m.

METHODS

Covariate Data Collection

We created a Geographic Information System (GIS) and used size, elevation (Skaar 1990), location (Skaar 1990, Kelly 1992, Paugh 2006), and water fluctuation (e.g. reservoirs or sloughs) as criteria to identify potential lakes for sampling. We removed lakes smaller than 5 ha (0.4 ha below the known lower limit for nesting lakes in Montana; Skaar 1990, Kelly 1992) and all lakes above 1524 m in elevation (Skaar 1990). We used ecological unit subsections (Nesser et al. 1997) in which loons nested to select lakes for sampling. We systematically removed lakes and sloughs connected to regulated rivers because of unnatural water level fluctuation which prevents natural nesting. We quantified characteristics of habitat, disturbance, and intraspecific interaction at each potential lake.

Lake Surveys

Since loons tend to remain at or near carrying capacity (Evers 2004), exhibit high territory fidelity (Evers 2001), and were monitored over the last 20 years in Montana, we assumed that the lakes we surveyed accounted for all potential breeding opportunities and variability in reproductive potential. They are an aggressive species with obvious territorial calls and displays, so that the presence of pair on a lake makes it likely to observe the pair or find its nest. Each field season we began searching for occupied lakes during the first week of May starting with lakes historically occupied by loons followed by the additional potential lakes. We surveyed lakes with 20X-60X spotting scopes. Large lakes with complex shorelines were surveyed by boat or kayak. Once we identified nesting lakes, we visited them every 4-8 days until the nest failed, the chicks hatched and died, or the chicks fledged. We assumed detection probabilities of fledged young equal to 1.0; however, to ensure we did not miss fledged young we visited all lakes that had chicks at the beginning of the season for one final observation during the final week of the field season (19-26 August 2007). Essentially, we could estimate hatch dates for all chicks and knew that chicks did not fledge until approximately 13 weeks of age. Therefore, if chicks survived to fledge they would be on their natal lake at the end of the summer and allow us an additional opportunity to detect fledged chicks. We did not detect chicks on lakes that were recorded as lost.

Modeling Potential Reproduction

We assigned variables into one of three model categories: disturbance, habitat, and intraspecific interaction. We also categorized variables as either lake or landscape scale (Paugh 2006). We used Pearson correlation coefficients to measure the relationships between all possible combinations of variables. For variables where $r \geq 0.6$, we chose to include only the variable that had the most biological meaning base on previous common loon habitat studies. We defined

potential territories as those lakes that were greater than 5 ha in size, less than 5000 ft in elevation, and generally located to the west of the continental divide. We developed a set of a priori candidate models and used generalized linear modeling (SPSS 15.0, Chicago, IL, 2006) to assess effects of disturbance, habitat, and intraspecific interactions on reproduction in common loons. We used Akaike's Information Criterion corrected for small sample size (AIC_c) to select which models were best supported by the data and ranked all models within categories and over all categories (Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2$ have substantial support while model with $4 \leq \Delta AIC_c \leq 7$ receive considerably less (Burnham and Anderson 2002). We used model weights to evaluate relative support among models, and model-averaged coefficients to reduce variability of predicted values and increase model-based inference for prediction (Burnham and Anderson 2002). We calculated variable importance as the sum of weights across all models where the variable occurred to assess the relative contribution of the covariates to the model (Burnham and Anderson 2002).

RESULTS

We observed 32 fledglings on 47 territories in 2006 (0.34 female chicks fledged/territorial pair) and 40 fledglings on 57 lakes 2007 (0.35 female chicks fledged/territorial pair). Our global model ranked 36th overall ($\Delta AIC_c = 12.63$, $R^2 = 0.196$). Habitat models ranked first while disturbance models were second with the highest ranking disturbance model ranked 6th overall. Intraspecific models received little support and the highest model ranked 12th overall ($\Delta AIC_c = 5.60$). In addition, models with landscape scale covariates received little support while models with lake scale covariates received considerable support.

Model selection identified 6 competing models ($\Delta AIC_c < 4$) which accounted for 71.4% of model weight and contained 6 individual variables. Model averaged coefficient estimates

revealed significant relations for islands and shoreline complexity (Table 3). The presence of islands was the most important variable (importance = 0.71) and had a negative effect on reproduction while shoreline complexity (importance = 0.27) had a positive effect. Disturbance had a weak positive effect on territory reproductive potential. Model with habitat variables were most important (0.93), while models with disturbance variables and intraspecific variables were of nearly equal importance (0.08 and 0.07, respectively).

DISCUSSION

Reproduction is a valuable measure as it provides insight into management recommendations at the individual lake level. Montana ranked 5th out of 13 common loon populations in North America (Evers 2004) with an average of 0.35 female chicks fledged/territorial pair which indicates a growing population. Our top 6 models explained little variation in the data suggesting we may not have captured all of the factors that explain reproduction in common loons. All of our top models contained habitat covariates, none contained intraspecific covariates, and only one model contained disturbance covariates. This suggests that all habitat covariates were important to reproduction; however, after closer examination we observed that islands essentially accounted for most of the model weight and adding additional habitat variables did not improve the fit of the model. It also suggests that lake scale covariates have considerable influence on reproduction while landscape scale covariates have little to no influence. In addition the numbers of territorial pairs within 10 km, abundance of feeding lakes, and distance to the nearest territorial pair have little to no influence on reproduction. Also, the role disturbance played in reproductions was ambiguous.

We assumed if nest success was higher on lakes where loon nested on islands then those territories would fledge more chicks than territories where loons nested on the main shoreline.

Yet, we found that common loon reproduction was strongly related to the absence of islands suggesting that territories without islands produce more fledglings. Similar observations were made in Maine with floating platforms (Lucas Savoy, Biodiversity Research Institute, ME 2008). We suggest similar to Barr (1996) and Piper et al. (2000) that decreased reproduction is the result of infanticide. We hypothesize that single birds cue in on chicks as an indicator of habitat quality and may kill chicks to curtail the defense behavior of the established pair. Models supported the positive effect of shoreline complexity providing additional support that lakes with complex shorelines offer critical foraging areas and nursery for loons to successfully raise their young and reproduction increased on lakes with more complex shorelines.

Many other effects of covariates on reproduction were supported by the data; however, their confidence intervals overlapped and were symmetrical around 0. The only factor that was not supported by the data was the effect of disturbance on reproductive potential. The model averaged estimate for disturbance was positive suggesting higher reproduction on lakes with higher disturbance. Caron and Robinson (1994) found a similar response to human activity in Upper Michigan, but these results and our results are contradictory to most research on the loon's response to disturbance (Vermeer 1973, Titus and VanDruff 1981, Paruk et al. 2000), and since the confidence intervals overlapped its effect was ambiguous. We hypothesized disturbance would have a negative effect on territory reproductive potential; however, our analysis did not support this hypothesis. We suggest that disturbance, as we measured, did not adequately capture a loon's response to disturbance. Our disturbance variable was mainly associated with shoreline disturbance and not with other types of disturbance such as watercraft use (i.e. fishing boats, jet skis, canoes, etc.). Also, disturbance may not be factor because of mitigation effort. The Montana Common Loon Working Group through interns with multiple partners provide

public education regarding loon nesting ecology on lakes with breeding loons, place floating signs to implement voluntary nest site closures, give campfire presentations, and collect vital information on lake use. We hypothesize that it is possible these efforts have been successful in mitigating the potential negative effects of disturbance on reproductive potential. Paugh (2006) offered similar explanations for nest survival and chick survival in response to disturbance after Kelly (1992) reported negative influences of disturbance.

We collected our data in a system where lakes ranged from loons generally occupied and defended small single lakes and we had very few large lakes containing multiple pairs. Other studies excluded small lakes from their analysis because they accounted for less than 5% of production (Croskery 1991). The density of common loons in our study was low (40-60 territorial pairs for 60,000 km²) relative to other regions of North America. For these reasons we suggest our models may not be appropriate for predicting reproduction in systems where numerous lakes have multiple pairs, especially if the number of pairs per lake exceeds 4 pairs.

MANAGEMENT IMPLICATIONS

Our results suggest that the factors that most influence reproduction by common loons in northwest Montana are the absence of islands and the complexity of the shoreline. Managers should protect shoreline habitat on lakes, especially those lakes that have complex shorelines. We recommend managers closely monitor lakes with islands to determine the causes of chick mortality and if changes in management strategies could increase reproduction. Conservation of shorelines in bays would be especially beneficial as these areas offer critical nursery areas for raising chicks. We suggest that the effects of disturbance were ambiguous because of past and present mitigation efforts and urge that future management strategies incorporate mitigation to

ensure shoreline disturbance does not become a negative influence on reproduction of common loons in Montana.

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Table 1. Definitions of disturbance, habitat, and intraspecific variables that we evaluated and their hypothesized effects on reproduction by the common loon in northwest Montana, USA, 2006-2007.

Table 2. Summary of model selection results ($\Delta AIC < 4$) for reproductive potential by the common loon on lakes in northwest Montana, USA, 2006-2007.

Table 3. Coefficient estimates (SE) from the model averaged model (Akaike wt = 0.714) describing reproduction for common loons, northwest Montana, USA, 2006-2007.

Figure 1. Common loon research area, Montana, USA, 2005-2007.

Figure 2. Means and 95% confidence intervals for reproduction on lakes with and without islands for the common loon, Montana, USA, 2005-2007.

Table 1.

Model Category	Variable Scale	Definition	Effects
Disturbance	Lake	Disturbance ratio of human development and recreation use on lake in relation to surface area	$\beta < 0$
	Lake	Disturbance ratio of human development and recreation use on lake in relation to perimeter ^a	$\beta < 0$
Habitat	Lake	Shoreline complexity	$\beta > 0$
	Lake	Presence of islands	$\beta > 0$
	Lake	Water clarity measure by Secchi Disk	$\beta > 0$
	Lake	pH	$\beta < 0$
	Lake	Lake surface area	$\beta > 0$
	Lake	Lake perimeter ^b	$\beta > 0$
Intraspecific	Landscape	Number of territorial pairs within 10 km	$\beta > 0$
	Landscape	Number of feeding lakes within 10 km	$\beta > 0$
	Landscape	Distance to the nearest territorial pair	$\beta > 0$

^a We excluded perimeter disturbance ratio from the analysis because of its correlation with the surface area disturbance ratio ($r = 0.62$).

^b We excluded lake perimeter from the analysis because of its correlation with lake surface ($r = 0.94$) and shoreline complexity ($r = 0.60$).

Table 2.

Model	K	AIC _c	Δ AIC _c	w_i
{FEC(Islands + Shoreline Complexity)}	3	36.01	0	0.27
{FEC(Islands)}	2	37.20	1.19	0.15
{FEC(Islands + Clarity)}	3	37.96	1.94	0.10
{FEC(Islands + Surface Area)}	3	38.78	2.76	0.07
{FEC(Islands + pH)}	3	39.07	3.06	0.06
{FEC(Islands + Shoreline Disturbance)}	3	39.19	3.17	0.06

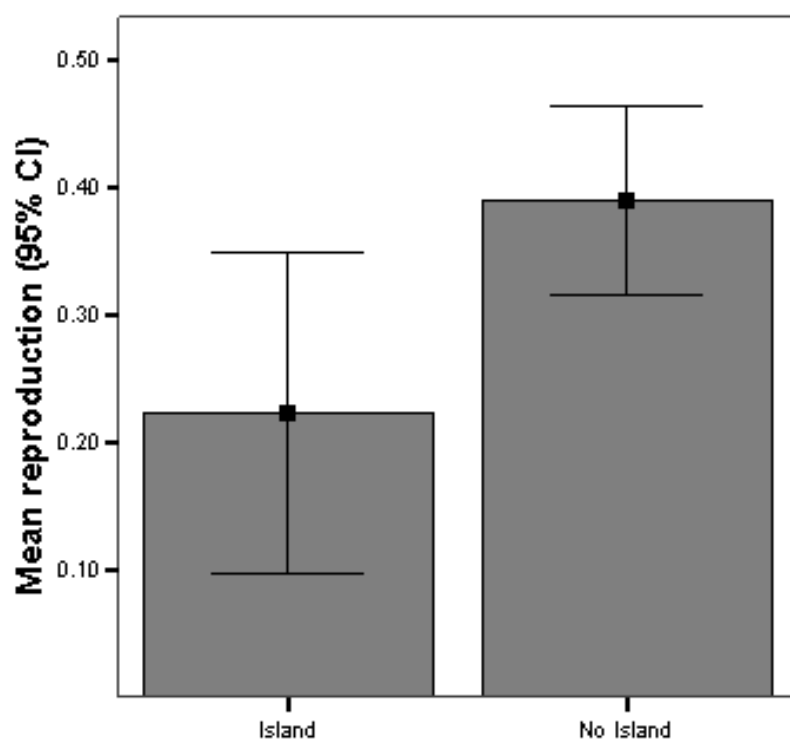
Table 3.

Covariate	Estimate	SE	Upper 90% CI	Lower 90% CI
Islands ^a	0.196	0.075	0.321	0.070
Shoreline				
Complexity	0.036	0.020	0.069	0.003
Clarity	0.003	0.002	0.007	-0.001
Lake Surface Area	0.002	0.004	0.008	-0.005
pH	-0.002	0.005	0.007	-0.011
Disturbance	0.004	0.013	0.026	-0.018

Figure 1.



Figure 2.



APPENDIX A

Survival Analysis

Objective

Estimates for survival exist for populations around the United States with the exception of Montana. Survival rates for common loons are considered high in most populations and are generally obtained using simplified methods (Evers 2001). The purpose of our analysis was to estimate breeding adult survival rates for Montana using a traditional mark-recapture analysis and compare our results to rates estimated using simpler methods and to other regions throughout North America. In addition we were interested in comparing adult male and adult female survival rates as in some species one would expect differences.

Methods

We analyzed banding data of 66 adult breeding common loons (30 males, 36 females) from 37 different territories in northwest Montana collected from 1996-2007. We used Cormack-Jolly-Seber open population models in Program MARK to estimate survival rates for breeding adults. We conducted a goodness-of-fit test on our data. We used Akaike's Information Criterion corrected for small sample size and overdispersion ($QAIC_c$) to rank all models (Burnham and Anderson 2002). Models with $\Delta QAIC_c \leq 2$ have substantial support while model with $4 \leq \Delta QAIC_c \leq 7$ receive considerably less, and models with $\Delta QAIC_c \geq 10$ receive no support (Burnham and Anderson 2002). We used model weights to evaluate relative support among models (Burnham and Anderson 2002).

Results

We found our data was overdispersed ($c\text{-hat} = 2.458$) and made appropriate adjustments. We also found that $p = 1$. The constant model $[\phi(.)p(.)]$ best fit our data and accounted for over 99% of the model weight. The second ranked model $[\phi(t)p(.)]$ received no support and had a $\Delta QAIC_c = 17.29$. Breeding adult survival estimates were high ($\phi = 0.90$, $SE = 0.022$). We found essentially no differences between sexes (male $\phi = 0.901$, $SE = 0.035$ and female $\phi = 0.899$, $SE = 0.029$). We produced nearly the same results using simpler methods described by Evers (2001) (male survival = 0.909, female survival = 0.895, and combined survival = 0.90).

Discussion

Adult survival for breeding common loons in Montana was high and comparable to other populations around North America. Survival estimates from populations in the Great Lakes Region and New England Regions averaged 0.91 (Evers 2004). Our analysis suggests that simpler methods can be used to obtain accurate estimates of breeding common loon survival rates especially when modeling under the condition that $p = 1$, which was our situation. In these cases return rates are equal to apparent survival.